Seasonal Migration and Population Regulation
in the Limpet *Acmaea (Collisella) digitalis*

BY

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(7 Text figures)

INTRODUCTION

The limpet species *Acmaea digitalis* Rathke, 1833 occupies a broad band within the intertidal zone, from near mid-tide almost to high tide level in the study area described below. Within this band are many different types of microhabitat, and superimposed are seasonal changes in physical and biotic conditions in the intertidal zone. The stresses placed on a species living in such a mosaic result in many adaptations that can be studied relatively easily.

Frank (1965), in an extensive study of a population of *Acmaea digitalis* in Oregon, found that behavioural adaptations are responsible for determining the vertical range and the size distribution at a given place within the range. He found that small limpets settle at the lower end of the shore and migrate upward in successive years, so that larger individuals tend to be found on the higher parts of the range. This has also been observed in a species of *Patella* in Britain (Lewis, 1954). Frank also found that local density of limpets appeared to be regulated by dispersing behaviour.

The object of this study, carried out in British Columbia in 1969 and 1970, was to examine further the relation between behaviour and population regulation. Two behaviour patterns were studied: homing and seasonal migration. Homing behaviour has been discussed in a previous paper (Breen, 1971); this paper deals with seasonal migration.

Many of the experiments and results described below confirm experiments carried out by Frank (1965). This paper is perhaps justified, however, in consideration of Frank's statement "what does a limited though extensive set of observations and measurements, gathered over a relatively short time span and in a small portion of the

species' range, signify regarding the performance of this and similar sorts of animals over their total area of distribution? These limitations ... clearly imply that independent confirmation of significant conclusions is particularly important."

ECOLOGY OF *Acmaea digitalis*

Physical Factors

This study was carried out on a rocky shore near Port Renfrew, British Columbia, known locally as Botanical Beach in reference to the Seaside Station maintained there by the University of Minnesota from 1900 to 1910. Botanical Beach consists of a broad sandstone shelf, intruded by hard metamorphic rock, which is up to 100 m wide at low tide. The shelf has been eroded into a complex array of pools, benches, and prominences. (Hall, 1906, gives a more complete geological description.)

Although the beach borders the Strait of Juan de Fuca, it is directly exposed to Pacific storms and wave action coming from the west and northwest, and is an exposed shore. Tides are mixed semi-diurnal, with a range of from 6.1 to 12.6 feet (1.8 to 3.8 m).

Tides, sea conditions and weather combine to produce a drastic contrast in shore conditions between winter and summer. In summer, lower low tide occurs between dawn and noon during most of the lunar cycle, and lower high tide in the afternoon. Summer weather usually includes long periods of hot, dry weather, so the shore is exposed to drying conditions during most of the day. The sea remains relatively calm. In winter, lower low tide occurs between dusk and midnight, while higher high tide occurs during the day, so the shore is covered during most of the daylight hours. Winter weather is cool and wet, with almost constant rainfall and fogs. Sea conditions are much

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Figure 2

Size frequency distribution of limpets at different tidal heights along a transect. Tidal height of each sample is given in parentheses

(adjacent column →)

rougher than in summer, and so the rocks are washed far above the actual tide height. The result of these factors is that the shore is never dry between mid-October and late spring, while during the summer it is generally dry during most of the day.

Freezing conditions, such as those observed by FRANK (1965) in Oregon, were not present during the winter encompassed by this study. The effects of very cold weather and ice on limpet populations could therefore not be evaluated.

DISTRIBUTION OF *Acmaea digitalis*

The distribution of *Acmaea digitalis* was determined quantitatively in May, 1969, by means of a transect on a gently sloping part of the shore which was partly protected from direct wave action. A line was laid down the shore and marked at 1 m intervals. Limpets were counted and removed from within 10 cm of the line, and were later measured. Tidal heights of points along this transect were
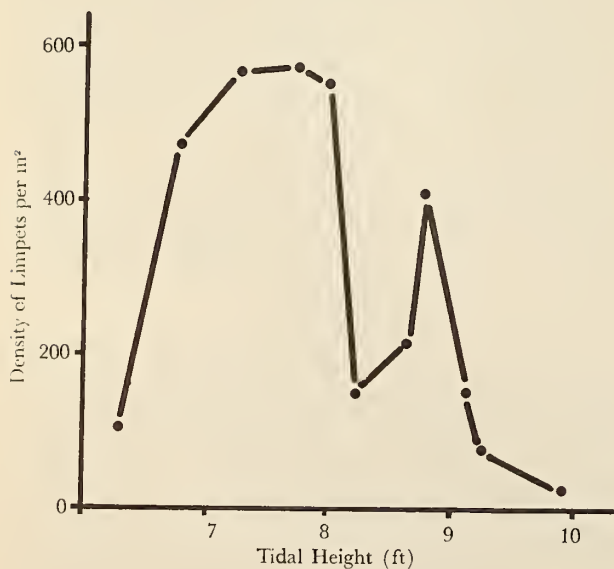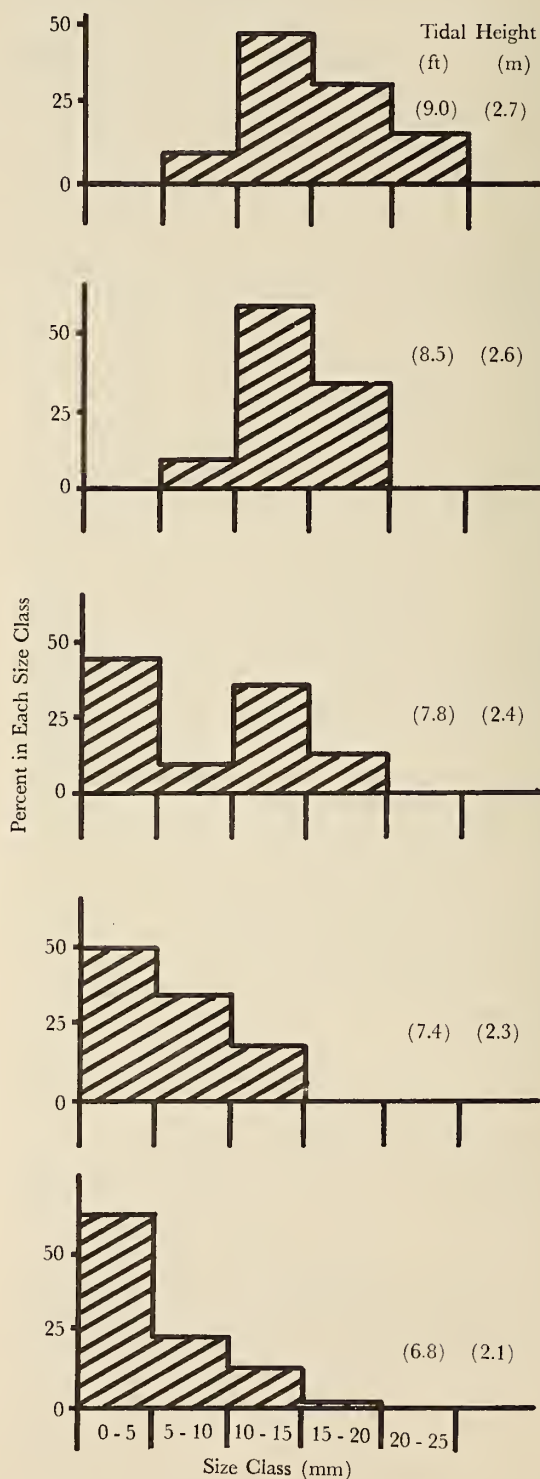

Figure 1

Density of *Acmaea digitalis* vs. tidal height along a transect

determined later, in conjunction with a mapping survey, by means of a surveyor's level.

Acmaea digitalis were found at this site from 6.0 to 10.0 tidal feet (1.8 to 3.1 m). Density of limpets along the transect is shown in Figure 1. Density reaches a peak at 7.2 feet (2.2 m) and then declines with increasing tidal height, except that around 8.5 feet (2.6 m) was found an abundance of small, shallow pools in which *A. digitalis* does not occur. Figure 2 shows the distribution of size frequencies at different heights. The modal size class increases with increasing tidal height. These observations agree with those of FRANK (1965), and support his suggestion that limpets settle at the lower end of the vertical range and migrate upward in successive years. Very small limpets (2 - 5 mm) began to appear in April and May, 1970, from 6.0 to 8.0 feet along the transect. It should be noted that in a steeper area more directly exposed to surf, the species occurred between 9.0 and 14.0 feet (2.7 to 4.3 m). Tidal height is thus only a relative measurement, subject to modification by local factors.

Although this was essentially a one-species study, the distributions of other species of limpets were noted casually on the transect site. *Acmaea pelta* Rathke, 1833 and *A. paradigitalis* Fritchman, 1960, occurred partially within the same vertical range as *A. digitalis,* but appeared to be mostly in pools and on very flat surfaces, whereas *A. digitalis* was found on sloping surfaces and almost never in pools. Very few limpets of other species were ever seen in *A. digitalis* aggregations. HAVEN (1971) found a division of habitat between *A. digitalis* and *A. scabra* (Gould, 1846) in California. *Acmaea scutum* Rathke, 1833, occurred only below 7.5 feet (2.3 m), and a slight overlap with the lower population of *A. digitalis* occurred.

DISTRIBUTION AND ABUNDANCE OF FOOD

In summer, few macrophytes occurred within the range of *Acmaea digitalis*, except for a few tufts of *Gelidium* sp. and *Fucus* sp., which the limpets did not appear to graze. A thin film of microscopic plants covered the substrate; when grazers were excluded the film thickened and proved to be composed of colonial diatoms.

In October, 1969, the thin film became a dense mat, composed of strands up to 3 mm long, covering most of the middle and upper intertidal zone. CASTENHOLZ (1961) observed a similar thickening of the mat in Oregon, and attributed it to a decrease in littorine density. At Port Renfrew the dense mat appeared in October even in areas where littorines had never occurred; so its appearance was not caused by a decrease in littorine abundance. An alternate explanation might be the change in physical conditions which occurred in October.

The diatom mat quickly disappeared in areas adjacent to dense aggregations of limpets and declined slowly in the other areas of the shore. After 4 months it had reached summer levels again, except in one place where there were no grazers at all; here it remained until March. Grazing, thus, is a likely cause of the mat's decline.

Individual *Porphyra* sp. settled on the upper intertidal zone in November, but quickly disappeared below 12.0 feet (3.7 m). Grazing by limpets and littorines might have been responsible for this disappearance. This alga remained above 12 feet until late spring.

From these observations it was inferred that the main diet of *Acmaea digitalis* consists of diatoms, and that food is most abundant during the period from October through March.

OCCURRENCE
OF SEASONAL MIGRATIONS

Two samples of individually marked limpets were used to determine whether or not seasonal migration occurs in the population at Port Renfrew. Both samples were
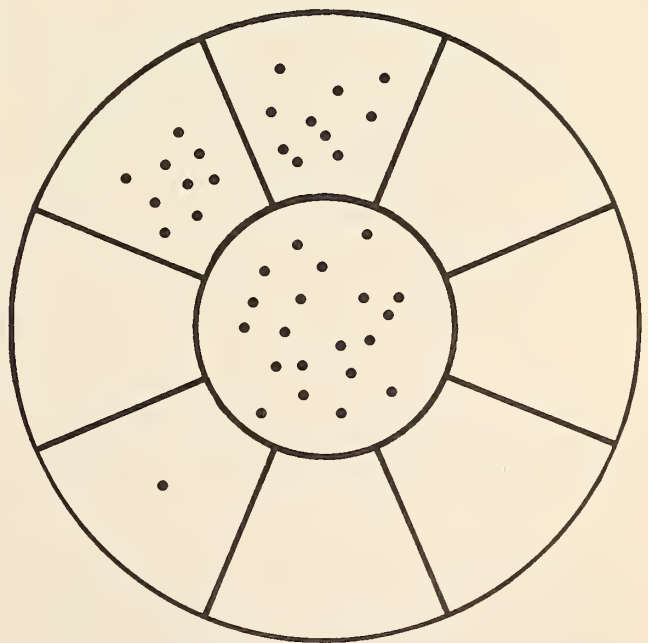

Figure 3

Directions of limpet migration during the period September 1, 1969 to February 16, 1970. Each dot represents one limpet; those in the centre circle represent non-migrants, those in the upper sector upward migrants, and so on

marked in early summer, 1969 (see BREEN, 1971, for discussion of marking technique). The positions of limpets were recorded in September, 1969, and February, 1970, with reference either to a fixed point on the rock (first sample) or to a grid (second sample). From these data the net fall and winter movement of each limpet could be determined. A limpet that remained within 1 m of its September position was considered not to have migrated.

Figures 3 and 4 show the directions in which migration occurred during this period. Although many limpets did not show net movement, an upward tendency was clearly demonstrated by migrants.

Figure 5

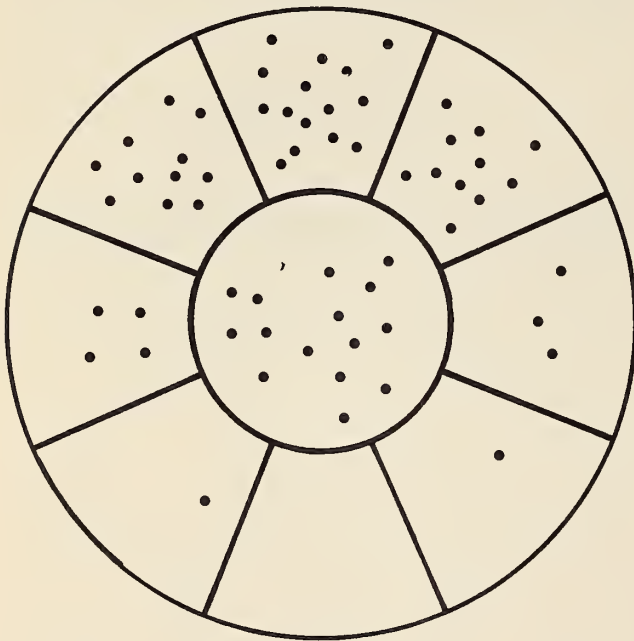Directions of limpet migration during the period February 16 to June 5, 1970

Figure 4

Directions of limpet migration during the same period as Figure 3 in a second sample

The positions of limpets in the first sample were again determined in June, 1970, and net movements between February and June were calculated. Although fewer limpets migrated during this period, a slight downward net movement was shown (Figure 5). It was concluded from this that seasonal migration does occur at Port Renfrew, with an upward migration in fall and winter and a lesser, downward migration in spring.
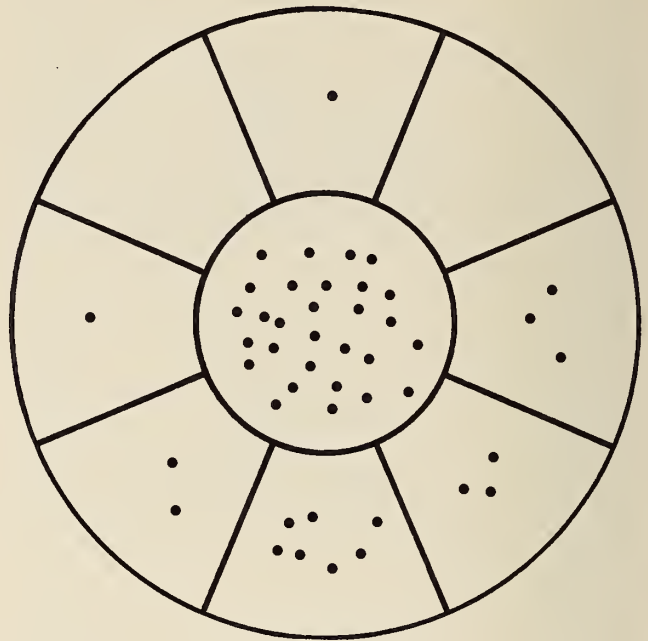
RELATION OF UPWARD MIGRATION WITH DENSITY

In June, 1969, an experiment was designed to test whether density affects the proportion of limpets which migrate from an area. A concretion was found on the shore which was 1.5 m across, 0.5 high, roughly circular and surrounded by a flat sandstone shelf. At the base of this, which was slightly concave, many limpets sheltered during low tide, and a few more were found on the top of the concretion. Two wedge-shaped areas were formed by placing 3 fences, of plastic mesh sealed to the rock with cement, from the top of the concretion out 1 m onto the sandstone shelf. Limpets within these two areas were then marked individually. The fences prevented lateral movements but allowed migration downward to the sandstone shelf and upward to the open top of the rock.

One area was designated a control group. Density of limpets in the other area was increased at intervals during the summer by the addition of unmarked limpets removed

from elsewhere, until in August it was 3 times the original density. The position of each marked limpet was recorded at monthly intervals; and shell lengths were recorded on July 5 and November 22, 1969.
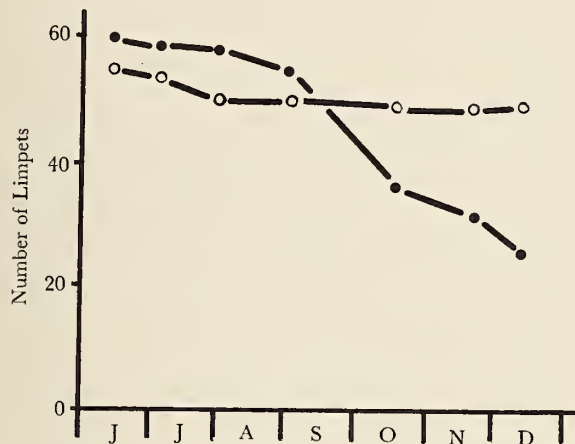

Figure 6

Number of limpets remaining in an experimentally crowded area (A) and in a control area (B) from June to December, 1969. (see text for explanation)

Figure 6 shows the number of limpets which remained in each area from June through December, 1969. Despite the large increase in density in the experimental area, most marked animals in each group remained until October. At that time the experimental group declined sharply, while the control remained relatively constant.

The change in the experimental group could have been caused by emigration, mortality, or both. A search was made for emigrant limpets in December, 1969, within a radius of 5 m from the concretion. One marked limpet from the control and 5 from the experimental group were found. It is known from other observations that limpets are capable of moving more than 5 m in a month, so these may not have been the only emigrants.

Mortality may have been partly responsible for the decline of limpets in the crowded group, since more than 30 limpets disappeared and only 5 could be found. It could be concluded, however, that emigration from the crowded group was greater than that from the control group, and that emigration did not occur until fall.

Growth rates of limpets in the two groups were compared by means of regressions of attained length on initial

length (Table 1). Limpets in the control group grew significantly faster than the crowded limpets during the period July 5 to November 22.

Table 1

A comparison of the growth rates of experimentally crowded limpets with those of a control group. The regression lines compared are those of attained length on initial length (Ford-Walford plot)

	Group	
	crowded	control
Regression equation	$Y = 0.28 + 0.85X$	$Y = 0.42 + 0.80X$
Sample size	31	42
F from comparing slopes	0.40 n. s.	
F from comparing adjacent means ($x = 1.74$)	7.45 [3]	

[3] significant at $\alpha = 0.01$

SUMMER MORTALITY

In May, 1969, when this study was begun, there were many attachment scars of limpets found in the high intertidal zone. This indicated that individuals recently present had either died or migrated away. The radical change in physical conditions on the upper intertidal area, between winter and summer, coupled with the observation that limpets migrate into the upper intertidal area from lower areas during winter, suggests that mortality should

Table 2

Tidal heights and original number of limpets in 6 areas used to determine survival rate from May 1 to July 26, 1970 (Figure 7). Limpets in the lowest area were counted in 2 groups: those assumed to be newly-settled (2 - 5 mm), and older ones. These are given as groups 6a and 6b, respectively

Group	Tidal Height		Number of
	(feet)	(m)	Limpets May 1
1	14.7	4.5	35
2	14.6	4.4	279
3	12.0	3.7	410
4	10.9	3.3	327
5	10.4	3.2	252
6a	9.4	2.9	287
6b	9.4	2.9	163

be high during summer as a result of warm dry conditions there.

This was tested by measuring survival in groups of limpets at different heights on the shore. Six permanent counting areas were marked on the rock in May, 1970, and all limpets in each area were counted periodically throughout the summer. As a check on migration from counting areas, some limpets in each of the upper 4 squares were marked with quick-drying paint, and searches were made for these outside the counting areas when counts were made. Emigration from counting areas was found to be negligible.

The tidal heights of each area (determined with a surveyor's level), original number of limpets in each and the percent survival are shown in Table 2 and Figure 7. The lowermost area contained both newly-settled limpets and older ones; these were counted separately and survival rates are presented for each. Survival was high in the lower 3 areas (either immigration to the areas occurred, or the initial counts were too low), but decreased with increasing tidal height. An exception to this pattern was seen in survival of newly-settled limpets in the lowermost area, which was the lowest of any group.

It was not possible to assign any one cause to the mortality observed in this group of observations. Direct effects of desiccation were tested in the following way: Limpets normally cling to the substrate sufficiently well that they are not dislodged by a tap on the side of the shell. Limpets weakened or dead, however, can be tapped loose from the rock. In July, 1969, after a period of dry weather and calm seas, limpets in the upper intertidal area were tested by using this 'tapping' method. Of several hundred tested, 75 were dislodged. These were placed immediately into cold seawater and examined half an hour later. Only 3 failed to revive in seawater. In 1970 the weather was cooler, and when the same test was carried out in July only very few limpets were dislodged. All revived when placed in seawater.

This crude test suggests that death resulting directly from desiccation is rare. Partly empty shells were some·times found in small groups on the shore at low tide, which suggested that predation was responsible. Possible predators observed included mink, mice, crows, gulls, and shore birds. During prolonged observations of crows and shore birds no limpet was ever seen being eaten. Mink and mice, however, could not be observed closely enough to determine what was being eaten.

Predation might account for high mortality in the upper intertidal area if limpets are made more vulnerable to predation as a result of desiccation. Frank (1965) observed a mouse removing limpets which were weakened by dry, hot weather, and suggests that mice probably cannot
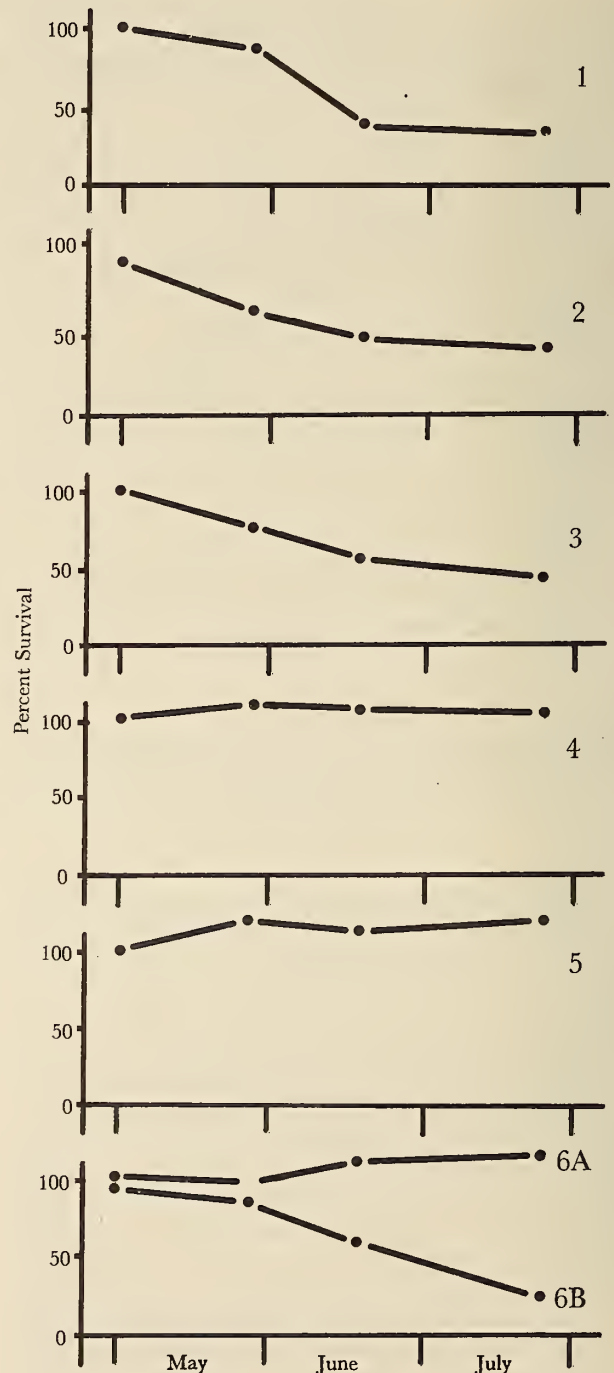

Figure 7

Survival of limpets from May 1 to July 26, 1970 in counting areas at different tidal heights. Tidal heights and the number of limpets originally present in each area are given in Table 2

remove a healthy limpet. Thus high mortality in summer might be considered an indirect effect of desiccation.

RELATION of UPWARD MIGRATION with GROWTH

Growth of limpets that had migrated from an area in fall and winter was compared with growth in the limpets which remained in the area. Length data were obtained from the two groups of marked limpets used to determine whether upward migration occurred at Port Renfrew and discussed above. Limpets in each group were measured in July, 1969, and again in February, 1970, so within each group the growth of limpets migrating in fall could be compared with growth in those that did not migrate (Table 3). (Within each group the initial lengths of migrants and non-migrants were compared and found to be statistically equal, thus a t-test was used to compare the growth increments.) In both groups the migrant limpets grew more than the non-migrants during fall and winter.

Table 3

A comparison between the mean growth increments of migratory and non-migratory limpets in 2 samples of marked individuals, from July 1, 1969, to February 16, 1970

	Group 1	
	migratory	non-migratory
mean increment (cm)	0.064	0.119
variance of increment	0.0037	0.0022
F ratio of variances	1.65 n. s.	
value of 't'	2.71 [4]	
	Group 2	
	migratory	non-migratory
mean increment (cm)	0.089	0.025
variance of increment	0.0056	0.0047
F ratio of variances	1.21 n. s.	
value of 't'	4.96 [4]	

[4] significant at $\alpha = 0.05$

Better growth of migrants can be explained in two ways. First, density is lower at higher shore levels, and since migrants in fall and winter tend to move upward they possibly encounter less intraspecific competition for food. Second, the size distribution changes with increasing tidal

height; larger size classes becoming more predominant. CASTENHOLZ (1961) found that large *Acmaea digitalis* are slightly less efficient at removing algae than smaller individuals. STIMSON (1970) found that the territorial species *Lottia gigantea* (Gray, 1834) does not graze down to bare rock, but leaves a thin film of algae. Smaller species, such as *A. digitalis,* outside *Lottia* territories graze down to bare rock, and Stimson suggests that *Lottia* would be outcompeted if it did not defend its territory. An alternate explanation for greater growth in fall migrants at Port Renfrew might be that small *A. digitalis* graze more efficiently than larger individuals; and thus the different size composition found at higher shore levels is responsible for better growth there.

An experiment was designed in February, 1970, to determine the better of these explanations. Three adjoined plots, each 65 cm square, were constructed with plastic mesh fences. The natural biomass of limpets within each plot was determined by removing all limpets and measuring their shell length. Shell length was then converted to body dry weight by means of a regression developed from 107 limpets for this purpose. This regression was

$$\log_e \text{ dry weight (g)} = -6.638 + 2.05 \text{ length (cm)}$$

The natural average biomass was found to be 6.87 g per plot.

Limpets 2.0 to 2.5 cm were collected from elsewhere, marked individually and measured. These were then added to the empty plots to form 3 treatments: (1) a control, consisting of enough marked limpets to equal the natural plot biomass, (2) a high density treatment, with double the natural plot biomass, and (3) a mixed high density

Table 4

Comparisons among mean growth increment of 3 groups of limpets (see text for explanation). The control mean is compared with the high density mean, and the high density mean with the mixed high density mean

Treatment	Control	High Density	Mixed High Density
number	25	30	26
mean growth increment (cm)	0.0048	−0.0417	−0.0677
variance of increment	0.00443	0.00208	0.00259
F ratio of variances		2.13 n. s.	1.24 n. s.
value of 't'		3.06 [5]	1.99 n. s.

[5] significant at $\alpha = 0.01$ (one-tailed), d. f. = 53

treatment, consisting of a biomass of marked limpets equal to the natural biomass, plus an equal weight of smaller (1.25 to 1.75 cm) limpets. These biomasses were calculated using the regression above.

Treatments were maintained in each plot from February 19 to July 24, 1970, when all marked limpets were removed and again measured. Growth in both high density plots was significantly lower than in the control (Table 4), but there was only a slight, non-significant difference between the 2 high-density treatments. This indicates that growth is inhibited by high densities, as already shown above, but that the size composition of competing *Acmaea digitalis* makes little difference in growth.

DISCUSSION

Of the two behaviours examined in this study, seasonal migration appears to be the more important with respect to regulation of local densities. Although the component parts of this regulating mechanism have been examined in the preceding sections, it has not been studied as a whole, so its operation as described below must be treated as an hypothesis.

Fall migration appears to be density-dependent in that the proportion of limpets which migrate from an area depends on the density in the area. This might partially regulate density at all levels of the shore in the following way: If heavy settlement were to occur at the lower part of the range of *Acmaea digitalis,* migration of older limpets from that area in fall would reduce density there. The older limpets that migrated would, in turn, produce an increased density in the area to which they migrated, and migration of the limpets originally there would be expected. Thus the heavy settlement of young might produce a wave of fall migration up the shore. Lesser settlement of young could be expected to have a lesser effect. Density at a given level of the shore might not be controlled within rigid limits in this way, but at least partial regulation could occur.

Conditions which produce high mortality are not present on the upper shore levels during fall, so these areas can be invaded by fall migrants. Migration is dependent on density, so the number of limpets which move to the highest levels depends on the density at lower levels. Mortality during the next summer among migrants on high parts of the shore can therefore be thought of as density-dependent in the population as a whole, even though it is independent of density in the area in which it occurs. For instance, if density on the shore is fairly low, few limpets will migrate onto the higher levels, and the proportion of deaths due to summer mortality will be low. If density is high, however, a higher proportion will migrate to the higher levels, and the proportion of deaths in the next summer will be greater.

The fact that high mortality occurs in summer at high shore levels, while lesser mortality occurs at lower levels, suggests at first that upward migration in fall is being selected against. Such selection might be outweighed, however, by the fact that fall migrants show better growth than non-migrants, probably because of reduced intra-specific competition for food. If fecundity is also increased for the same reason, a selective advantage of upward migration can be postulated. It might be possible for a limpet that migrates onto the high intertidal area to leave more offspring, as a result of increased fecundity, than a limpet that does not migrate, even if the migrant dies during the next summer and the non-migrant survives. Newly-settled *Acmaea digitalis* observed in April and May indicate that breeding occurs in late winter or early spring, after the time at which food is most abundant. This is between the times of upward migration and summer mortality, so the selective advantage just postulated seems possible.

FRANK (1965) found high winter mortality at the lower part of the shore and high summer mortality at the higher part. He suggests that seasonal movements, upward in fall and downward in spring, are an adaptive response to such mortality patterns. Migration may have evolved in response to other factors as well. It was noted earlier that settlement of *Acmaea digitalis* from the plankton occurred only below the 8 foot tidal level at Port Renfrew. A probable explanation for this is that small limpets cannot withstand desiccation as well as larger ones (DAVIES, 1969). A critical tide level (DOTY, 1946) might occur for newly-setted limpets, which ceases to be critical after they have grown larger and can withstand longer exposure to drying.

Thus upward migration might be an adaptation allowing limpets, as they grow, to exploit habitats which were previously unsuitable. It would be advantageous for a limpet to migrate upward whenever possible because of the lower density at higher levels, and hence the better opportunities for growth there.

Downward migration obviously cannot be explained in these terms, and FRANK's (1965) suggestion may be correct. It is important to note, however, that downward migration does not completely solve the problem of summer mortality, because net movements after migration are upward. This would suggest that, if both types of migration are advantageous in some respect, upward migration is more advantageous. If one considers only those factors dealt with here, this seems reasonable because migration upward confers the advantage of better opportunities for

growth at virtually all shore levels. Migration downward is advantageous only at the upper levels of the shore where summer mortality is a serious factor.

Results from the crowding experiment show that limpets tend to be conservative in movement during summer, and migrate from crowded areas only when conditions change in the fall. Dangers from desiccation are presumably serious enough in summer that, even in very crowded conditions, limpets prefer to remain in familiar territory where shelter is assured rather than seek out less crowded areas. For this reason, seasonal migration is probably more important in population regulation than homing behaviour.

Homing is possibly an adaptation to reduce the risk of desiccation, such as aggregation behaviour is (MILLARD, 1968). HAVEN (1971) suggests that this is the case in *Acmaea scabra* in California. This could be tested by measuring the degree of homing in *A. digitalis* at different levels and at different times. The expectation would be that homing increases at higher shore levels and is greatest during the warm, dry months, even in those limpets that do not migrate seasonally.

A great deal of emphasis has been placed above on desiccation as an important factor of the environment of *Acmaea digitalis*. This approach provided the basis for a possibly acceptable conceptual model of how populations adapt to variation in space and time. It must be emphasized, however, that other factors might be equally or more important in producing adaptations within this species.

ACKNOWLEDGMENTS

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